Bulletin of the Museum of Comparative Zoology

HARVARD UNIVERSITY

Vol. 131, No. 4

# THE BRAINCASE OF THE PALEOZOIC ELASMOBRANCH *TAMIOBATIS*

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With One Plate

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

April, 1964

Bull. Mus. Comp. Zool., Harvard Univ., **131**(4):87-105, April, 1964

# No. 4 — *The Braincase of the Paleozoic Elasmobranch* Tamiobatis

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## INTRODUCTION

Eastman in 1897 described, as *Tamiobatis vetustus*, a specimen from Powell County, Kentucky, enclosed in a limestone nodule, which he believed to exhibit the dorsal surface of the braincase of a Devonian skate. However, the age of the specimen is uncertain; it is not a skate; it is the ventral, rather than the dorsal surface of the braincase that is exposed. In consequence, Eastman's structural identifications are quite erroneous. The *Tamiobatis* type is, nevertheless, of considerable importance, for it is the best preserved specimen of a Paleozoic elasmobranch braincase so far described. A few Paleozoic forms are represented by crushed slab materials in which little morphological detail can be made out. But of three-dimensional Paleozoic shark braincases, there have been described only two imperfect specimens. These are partial, late Devonian braincases, presumably of "*Cladodus*" type (Stensiö, 1937; Gross, 1937).[1]

Some years ago I was struck by the obvious resemblance of *Tamiobatis* to the pleuracanth braincases which I was then studying. The specimen (USNM No. 1717) was loaned to me through the courtesy of the Division of Vertebrate Paleontology of the United States National Museum. In earlier years complete development of the specimen would have been extremely difficult; thanks, however, to the newer methods of acid preparation developed at the British Museum by H. A. Toombs and A. E. Rixon, the limestone nodule has been completely etched away without harm to delicate surface structures of the braincase. Preparation was done with the aid of a National Science Foundation grant for study of Carboniferous vertebrates. I had originally planned to defer description of this specimen until after publication of work on the structure (internal as well as external) of the pleuracanth braincase. But since it currently appears that this study will not be completed for some time to come, I am publishing the present account, despite the fact that incomplete knowledge of the internal structure of

[1] A further Paleozoic shark braincase is currently being studied by Dr. D. H. Dunkle of the U. S. National Museum.

older elasmobranch braincases may cause misinterpretation of the nature of foramina and other external features.

In the description below I have made no reference to Eastman's original description, since his belief that the originally exposed surface was dorsal rather than ventral invalidates his identifications. Thus, for example, the canals for the aortæ are identified by him as endolymphatic ducts, the pituitary fossa is said to be a dorsal fontanelle, the interorbital region is labelled rostrum, and the postorbital and otic processes are described as antorbital and postorbital processes, respectively.

### Provenance of the Specimen

No data concerning the discovery of this specimen have been preserved in the records of the U. S. National Museum beyond the statement that it was found in the eastern part of Powell County, Kentucky. As may be seen from a geological map (Jillson, 1929), this small county includes strata ranging from Silurian at its western margin to lower Pennsylvanian (Pottsville) on the ridge-tops to the east. However, the stratigraphic possibilities can be readily narrowed down. On the one hand, the Pennsylvanian beds are continental shales and sandstones, and it is practically out of the question that a limestone nodule containing marine vertebrates could have been derived from them. On the other hand, Silurian and most Devonian beds are confined to the western part of the county, and the only Devonian strata reaching the eastern part of Powell County are the black shales of the late Devonian, in which (again) occurrence of a limestone nodule of this sort is most unlikely.

Considerable work in this general area is being done at the present time by the U. S. Geological Survey. It is the opinion of those familiar with the region that the specimen rather surely came from early Mississippian limestones present in eastern Powell County. Possibly a closer determination can be made when current studies of the region are completed.

## DESCRIPTION

*General.* The general appearance of the braincase is readily seen in the illustrations. The surface of the cartilage was calcified to the extent of a millimeter or so. The calcified areas are dark in color; over a considerable area of the ventral surface, exposed before collection, the calcified material has been eroded, leaving a cast of the underlying region occupied by hyaline cartilage. Such areas are left white in the plate. The general proportions are obvious from either dorsal or ventral aspects, and such structural features as nasal processes, postorbital processes, the long otic region, with prominent lateral otic processes,

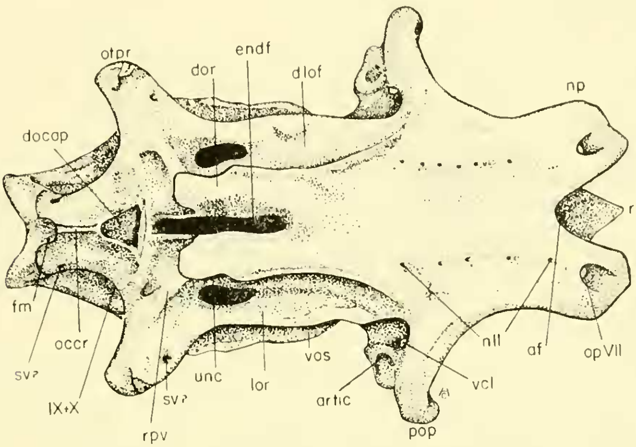


Fig. 1. Dorsal view of the braincase, slightly restored. × ½. Abbreviations for this and following figures: *af*, posterior border of anterior fontanelle; *artic*, articular facet for palatoquadrate; *cc*, point of entry of "common carotids" into braincase floor; *dlof*, dorsolateral otic fossa; *docop*, dorsal "opening" in occipital region; *dor*, dorsal otic ridge; *ec?*, impression of course of external carotid; *efh?*, foramen possibly for efferent hyoid artery; *endf*, endolymphatic fossa; *fm*, foramen magnum; *ic*, impressions of course of internal carotids toward pituitary region; *lor*, lateral otic ridge; *?mcv*, foramen probably for middle cephalic vein; *nll*, openings for supraorbital lateral line nerve twigs; *np*, nasal process; *occr*, occipital crest; *op V + VII*, foramen for ophthalmic rami of nerves V and VII; *op VII*, foramen for ophthalmic ramus of nerve VII; *os*, optic stalk; *otpr*, otic process; *pit*, pituitary region (eroded); *pop*, postorbital process; *pt VII*, canal for pretrematic ramus of nerve VII; *r*, calcified floor of base of rostrum; *rpv*, ridge covering posterior part of posterior vertical ear canal; *sos*, subocular shelf; *sv?*, foramina possibly for somatic nerve twigs; *unc*, uncalcified areas of braincase surface; *vcl*, foramen primarily for vena capitis lateralis; *vlof*, ventrolateral otic fossa; *vos*, ventral shelf in otic region containing passage for lateral head vein; *II*, optic foramen; *III*, oculomotor foramen; *IV*, trochlear foramen; $V_2 + V_3$, foramen for maxillary and mandibular rami of trigeminal nerve; $V_3$, groove for mandibular ramus of trigeminal; *VI?*, probable foramen for abducens nerve; *VII*, foramen for main trunk of facial nerve; *IX + X*, fossa for glossopharyngeal and vagus nerves.

and the occipital region, are apparent at first glance. A notable contrast with typical modern shark braincases is the long otic region. It seems quite certain that the braincase has undergone considerable dorsoventral crushing, so that the height (particularly in the otic region) is surely much less than was the case in life.

*Nasal region.* Anteriorly, as in modern sharks, the roof is deeply incised by the curved posterior margin of the anterior fontanelle, lying above the cavum precerebrale. Ventrally there is preserved, imperfectly, a thin sheet of calcified cartilage which represents a rostral structure. From its feeble nature it seems certain that the rostrum was short. On either side of the fontanelle the upper surface of the braincase extends anterolaterally to form a partial roof for the nasal region; a prominent foramen here is obviously for the emergence of the superficial ophthalmic ramus of nerve VII, innervating the lateral line organs of the snout.

Nasal capsules are not preserved and were presumably uncalcified. A nasal process is completely preserved on the right side; that of the left side is slightly imperfect anteriorly and laterally. From the tip of each process a narrow plate of calcified cartilage descends ventrally and posteromedially toward the floor of the braincase; this marks the anterior end of the plate of calcified cartilage which forms the inner wall of the orbital cavity and separates the orbit from intra-cranial areas. There is no foramen for an olfactory nerve in the anterior part of this plate, and hence this nerve lay medial to it and to the nasal process. The contours of the outer surface of this plate give no indication of the development of a nasal capsule lateral to it. It is hardly possible that the capsules could have been situated medially to these plates, filling — or nearly filling — the precerebral cavity. It seems reasonable to believe that these structures, not improbably essentially spherical in shape, projected forward, with the curved surfaces presented by the lateral edge of the rostrum and the plates descending from the nasal roof marking part of their ventral and lateral margins.

*Orbital region.* The braincase roof is very broad and nearly flat between the large orbits. On either side, the roof extends outward as a wide shelf, with a smoothly concave lateral outline, over the orbital cavities. A series of small foramina on either side allowed the passage of nerve twigs from the ophthalmic ramus of nerve VII to reach the neuromasts of the supraorbital lateral line canals.

Beneath this protecting roof, the upper part of the orbital wall shows a smooth sweep of its surface from the nasal region backward and, finally, outward to the anterior surface of the postorbital process. The superficial ophthalmic ramus of nerve VII obviously travelled forward well up beneath the roof (where are seen the inner openings of the small foramina for the supraorbital lateral line), to reach anteriorly the large foramen by which it gained the roof of the nasal region.

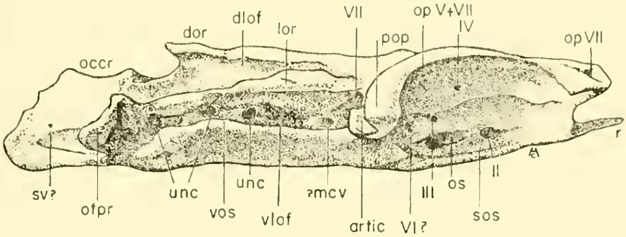


Fig. 2. Lateral view of the braincase, slightly restored. No attempt has been made to correct the marked dorsoventral crushing. Abbreviations as in Figure 1. $\times 1\frac{1}{2}$.

High up, posteriorly, is a large opening, directed anteriorly, which is surely for the exit of the ophthalmic rami of the trigeminal and facial nerves. Somewhat anterior and ventral to this is a small foramen in the appropriate position for emergence of the trochlear nerve and, farther ventrally, a somewhat larger foramen for the oculomotor nerve. Anteriorly, at about this vertical level, there develops a longitudinal ridge running forward toward the nasal region. Below this ridge there is present well anteriorly a large foramen, opening anterolaterally, which is presumably for the optic nerve. A narrow bar back of this foramen separates it from a long oval opening extending back much the length of the orbit not far above the floor. The upper and lower rims of this opening are somewhat everted; its posterior margin is curved strongly outward, and represents the anterior end of a swollen ridge which posteriorly subsides into the general contours of the cranial wall. The impression gained from this topography is that the opening provided for the emergence, anteriorly and laterally, of a cylindrical structure of some sort — obviously an eye stalk of typical elasmobranch type.

Openings for an ophthalmic (orbital) artery and a pituitary vein would be expected in the ventral part of the orbital cavity. I have been unable to make out such openings, presumably because of the crushing undergone here by the specimen.

Posterior to the position of the eye stalk, opposite the base of the postorbital process (and hence not seen in lateral view, but see Fig. 3A), there is a deep ventral recess, expanding anterolaterally from a large foramen. This was obviously for the emergence of $V_2$ and $V_3$ as well as, presumably, the lateralis nerves for the infraorbital and mandibular lateral line organs. Identification of a small imperfection in calcification as a foramen for nerve VI is less certain.

Ventrally, the orbital rim turns sharply outward to form a subocular shelf; this is far narrower than the dorsal rim. Anteriorly, the ventral surface of the braincase has been badly eroded, and it is possible that in life this shelf may have been more developed than the specimen now suggests.

*Postorbital process.* This process is highly developed. Its dorsal surface is convex in section, the anterior portion being a lateral continuation of the orbital roof. It curves markedly downward laterally. The anterior surface, conforming to the spherical contour of the orbit, is essentially a smooth wall, vertical below, curving outward above (Fig. 3A). From the ventral base of the anterior surface of the process a distinct groove, bounded below by the subocular shelf, extends outward for some distance. This may have served as a channel for the mandibular ramus of the trigeminal nerve. Distally, the postorbital process proper curves forward as well as downward. Back of this area

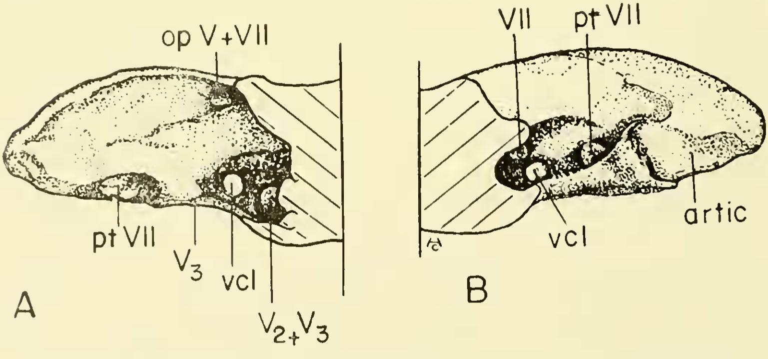


Fig. 3. *A*, anterior, and *B*, posterior views of the right postorbital process. Abbreviations as in Figure 1. × ½.

(Fig. 3B) is a well-defined articular surface, concave in cross section, for the palatoquadrate. Its curved anterodorsal boundary is the posterior border of the postorbital process proper, its ventrolateral boundary a ridge situated on a posterior accessory buttress of the postorbital process. Posteriorly, proximal to the articular area, the postorbital process is pierced diagonally by a prominent foramen. Its median opening enters the process well ventrally on the posterior surface; it emerges on the anterior surface just above a lateral extension of the subocular shelf. This foramen may have served for the passage forward of the pretrematic ramus of the facial nerve. At the base of the process a large foramen, surely carrying the vena capitis lateralis, pierces it in an anteroposterior direction. This leads from the ventral part of the orbital area, dorsolateral to the foramen for $V_2$-$V_3$, back to a ventrolateral shelf area in the otic region.

*Otic region.* As noted above, the otic region is very long, as compared with that of modern elasmobranchs. Even excluding the occipital region from comparison, the length here is much in excess of the anterior portion of the braincase. It is broad as well as long (although the seeming relative breadth is undoubtedly exaggerated because of dorsoventral crushing). For much of its length the median roof area is slightly concave in section — this a continuation of a slight median depression present in the interorbital region. Medially in the posterior half of the roof is an elongate fossa which obviously included the openings of the endolymphatic ducts. Posteriorly, this opening is surrounded by a low raised ridge; for most of its length, however, it is bordered by a pair of prominent ridges, which may be termed the dorsal otic ridges. For the anterior two-thirds of their lengths these ridges have laterally a sharp curved border, somewhat concave in outline in dorsal view. This may have lain parallel to the upper inner margin of the palatoquadrate, with which it may have had a ligamentous connection. Posteriorly, the processes become narrow, and are mildly swollen on their dorsal surfaces. Distally, their terminations overhang somewhat flattened areas on either side of the posterior end of the endolymphatic fossa; these areas were presumably occupied by median dorsal segments of the axial musculature, and the tips of the processes may have been in continuity with some type of "nuchal" ligaments. As shown by sections of pleuracanth braincases (similarly built in this region), the anterior vertical canals of the internal ear lay beneath the anterior portions of the dorsal otic ridges, and part of the posterior vertical canals lay beneath the posterior portion of the ridges.

Projecting laterally, the length of the otic segment, is a longitudinal ridge, rounded in section, which may be termed the lateral otic ridge. As shown by pleuracanth specimens, this lateral ridge contained the horizontal canal of the internal ear — a canal of remarkable length. Between dorsal and lateral otic ridges is a deep longitudinal hollow, which may be termed the dorsolateral otic fossa. The posterior boundary of the fossa is a low rounded ridge which descends posterolaterally from the dorsal otic ridge; this presumably overlies the posterior end of the posterior vertical canal. In the floor of the fossa is an oval area, broader posteriorly, in which no calcification of cartilage is present. I believe that this represents merely an absence of calcification in the surface cartilage in this region; it is improbable that any opening was present here in life. No further openings are apparent in the boundaries of the dorsolateral otic fossa. It may have been partially occupied by axial musculature.

Below the lateral otic ridge is a second longitudinal channel, which we may term the ventrolateral otic fossa. Its dorsal border is the lateral otic ridge; its floor a lateral extension of the basicranial floor, which curves upward as well as outward. This upward curvature results in the formation of a longitudinal trough which extends most of the length of the fossa; its outer margin is somewhat concave in contour as seen from above or below, although with a slight lateral projection (possibly post-mortem) at mid-length. Posteriorly this trough, which obviously carried the vena capitis lateralis, opens laterally somewhat short of the end of the otic region. Above the level of the trough and just behind the postorbital process a well-developed foramen opens outward and backward. This is undoubtedly the opening for the facial nerve. An opening posteroventral to this is perhaps for a middle cephalic vein. Farther posteriorly there are, on both sides of the specimen, two oval uncalcified areas on the inner wall of the fossa. I cannot interpret them as being to any degree functional; they are too far anterior for either to be reasonably interpreted as for nerve IX.

Posteriorly, on either side, the otic region expands laterally into a prominent lateral otic process. The dorsal surface of the process is for the most part gently convex; its proximal part was presumably underlain by the posterior end of the horizontal semicircular canal. Close to its anterior end is a tiny dorsal foramen which may have carried some component — ?somatic — of the IX-X nerve complex. The distal end of the process and the distal part of its anterior margin terminate in thin blunt ridges which would appear to have been articular in nature, perhaps having contact with some anterior member or members of the gill arch series of cartilages. The anterodistal terminus of the process is tilted prominently upward.

A very considerable part of the anterior face of the lateral otic process is lacking in calcification; this area is quite irregular in outline, as may be seen in the figures. But no reason can be adduced for such a prominent lack of chondrification. It is improbable that the condition seen in the specimen was due to post-mortem loss of surface, for this region was not exposed to weathering of the nodule, and despite the irregularity of the "opening" here, closely similar patterns are present on both sides.

As noted below, the under side of the otic process is deeply undermined posteriorly. On either side, the calcified base of the otic process is separated from the basal plate of the braincase by a narrow slit in which no calcification is present. Whether this slit existed in life, and represents a persistent marker between otic and occipital cartilages, or whether this is due to post-mortem crushing, is uncertain.

*Occipital region.* This is relatively short, constricted in width posteriorly, and of lesser depth than the otic region. Dorsally, indications of division betwen otic and occipital regions are seen in the form of slight ridges which begin, on either side, lateral to the posterior end of the endolymphatic fossa and curve outward and backward to the posterior margin of the base of the otic processes. Certain of the markings here are apparently post-mortem in nature, but probably represent, in any event, indications of structural weakness at the points of fusion of elements embryologically discrete. (No indications of separation of units are visible ventrally.)

Just posterior to a low transverse ridge behind the endolymphatic fossa is a large triangular opening, facing dorsally. At first glance one would assume, from its position, that this is the foramen magnum. This, however, is not the case, but the nature of this opening is unknown. Possibly it merely represents an uncalcified area in the braincase roof, but against this interpretation is the fact that the opening shows a distinct, if low, boundary ridge. Posterior to this opening there is a median occipital crest (incompletely preserved in the specimen). Below the posterior termination of this ridge lies the foramen magnum; this is nearly completely obscured by dorsoventral crushing. The dorsal portion of the occipital segment is relatively narrow, its lateral boundaries curving medially and posteriorly from the posterior margin of the otic processes. This dorsal area, bounding laterally the triangular dorsal opening, described above, and the occipital crest, is gently convex in vertical section; there is present here a small foramen, perhaps for a "spino-occipital" somatic nerve ramus.

Farther ventrally the occipital segment is much broader than it is dorsally, its lateral margins curving inward and then backward, from a point well out beneath the otic processes. The upper surface of this thin ventral region forms the floor of a cavity of considerable size which extends forward, contracting in width in its course, beneath the main expansion of the otic process and the dorsolateral margins of the occipital segment. This cavity was not explored to its full depth, but surely formed the exit for the vagus nerve and not improbably the glossopharyngeal as well. I believe I can make out, in the lateral wall of the cavity near its posterior end, the inner opening of the small foramen in the otic process, mentioned above, which may have carried a small somatic branch of the glossopharyngeal or vagus.

The occipital condyle is, as preserved, much broader than high; it is V-shaped in contour as seen from above or below, and deeply indented centrally, presumably for the notochord.

*Ventral surface.* The ventral surface of the specimen was exposed when found and had been subject to weathering. The light-colored areas shown in the plate are regions in which weathering had removed the thin surface calcification of the braincase floor; except anteriorly the damage was not severe. The ventral surface was essentially flat. In the interorbital region the lateral margins follow the curved line of the shelf underlying the orbit which, as noted earlier, has been destroyed in part by erosion. Behind the postorbital processes the floor broadens greatly, its lateral borders curving upward somewhat to form the margins of the trough which carried the vena capitis lateralis. Beyond the otic process there is a moderate constriction in width to the margins of the condyle. As suggested by the pattern of erosion, there were slight longitudinal ridges on either side of the midline toward the back; these merged anteriorly.

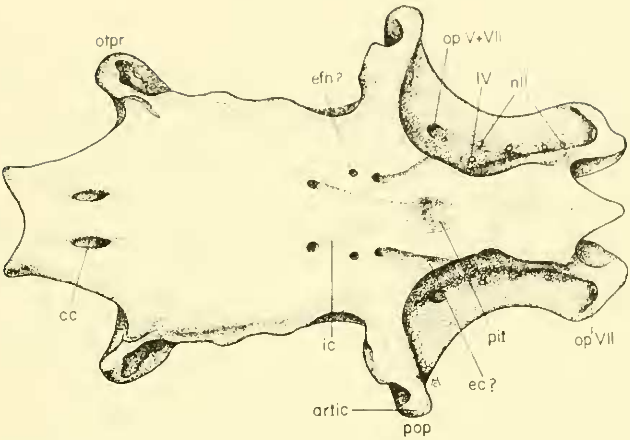


Fig. 4. Ventral view of the braincase; the pituitary region is imperfectly preserved. Abbreviations as in Figure 1. × ½.

Posteriorly the braincase extends to a greater depth than in typical modern elasmobranchs, for the paired anterior continuations of the dorsal aorta ("common carotids") entered the braincase floor a short distance anterior to the condyle. Well forward in the otic region a pair of openings presumably mark the exit of the carotids from the aortic canals, and, as may be seen from the plate, there is evidence of grooves — presumably for internal carotids — leading from these foramina forward and medially toward the hypophysial region. Farther forward on each side is a foramen which may have been the point of entrance of the hyomandibular (pseudobranchial) artery. Still farther forward on either side is a further opening, from which a deep groove leads forward and outward into the orbit; presumably this was for an external carotid.

It is unfortunate that almost the entire surface layer of calcified cartilage has been lost in the hypophysial region; however, it is reasonable to believe that the surface of the matrix essentially follows the surface contours. There was here a large oval depression, which may have contained an open hypophysial pit. Paired indentations leading forward from the front end of this depression suggest that the two internal carotids entered the braincase independently here.

## COMPARISONS

As noted above, uncrushed Paleozoic elasmobranch braincase material exists otherwise only in the case of the two late Devonian specimens of "*Cladodus*" and the pleuracanth material from the Permian which I am currently studying. The *Tamiobatis* type may be compared with these forms.

The specimen studied by Stensiö (1937) and named *Cladodus hassiacus* by Gross (1937) includes only the ventral half of the middle portion of the braincase. The roof is nowhere present; the specimen ends anteriorly without including the front borders of the orbit and terminates posteriorly part way along the otic region. As far as preserved, the general proportions are comparable to those seen in *Tamiobatis*. The optic nerve, eye stalk, main trigeminal opening, and more dorsal opening for ophthalmic rami are present as in *Tamiobatis*, but the last two foramina are apparently less developed than in our type. Due to crushing and erosion, I cannot tell whether or not *Tamiobatis* had a notch for palatoquadrate articulation (*obf* in Stensiö's figure 1) or whether the ventral bloodvessel openings which he figures were present. Stensiö has restored the nasal region directly from *Chlamydoselachus*, but there is no specific reason for assuming that the pattern was of the fashion found in that modern genus. Of the postorbital process only the lower portion was present in his specimen, and, probably as a consequence, it appears to be slimmer than in *Tamiobatis*. Quite surely, had the process been better preserved, there would have been found, as in *Tamiobatis* and in Gross' specimen, an articular facet for the palatoquadrate, and not improbably a canal of the sort which I have suggested as carrying the pretrematic ramus of the facial nerve (perhaps the notch which he illustrates at the tip of his postorbital process represents the remains of this canal). Stensiö in his figure 3 shows, on the left side, two canals emerging posteriorly from the base of the postorbital process, of which the upper is labelled as for the jugular vein, the lower for the main trunk of the facial nerve. The course indicated for the jugular is in an unusually high position for that vein, and I suggest that with better material it would be found that (as in *Tamiobatis*) it is the ventral canal which carries the lateral head vein and that the dorsal opening is that for the facial nerve.

As indicated by his figure 5 and the text, the canal region of the ear was incompletely preserved in Stensiö's specimen. Apparently parts, at least, of all three canals were present in his specimen. However, they appear to occupy a short space anteroposteriorly — much shorter than is the case in pleuracanths, *Tamiobatis*, or (apparently) in Gross' specimen of "*Cladodus*." This seeming abbreviation may well be due to crushing and imperfections at the posterior end of Stensiö's specimen.

In Stensiö's, as in Gross' specimen, in *Tamiobatis* and in pleuracanths, and in contrast with Recent elasmobranchs, the "common carotids" are carried well forward ventrally in the base of the braincase. A series of foramina farther forward in the braincase floor agree well in general with those described by Gross and those present (in incomplete fashion) in *Tamiobatis*.

Stensiö's specimen is incomplete posteriorly; he arbitrarily terminates the braincase in his figure 6 at a distance from the orbit comparable to that seen in modern elasmobranchs. Due to this arbitrary posterior termination, and to his restoration of the nasal region in accordance with that of *Chlamydoselachus*, the general picture of the braincase in his figure 6 is very similar to that of modern sharks. But quite surely better preservation of the specimen would have shown very different proportions, much more in keeping with Gross' *Cladodus wildungensis*, *Tamiobatis* and pleuracanths. In this instance, as in the further specimens to be discussed, certain features (the presence of an optic stalk, etc.) are closely comparable to those in modern elasmobranchs; others (as the canals for the "common carotids") are features probably of a primitive nature, lost or modified in modernized forms.

The specimen studied by Gross (1937) and referred to *Cladodus wildungensis* is from the same horizon and locality (Wildungen) as that of Stensiö, and considered by him to be generically identical. It is much more complete. Anteriorly, it includes the posterior margins of the dorsal fontanelle, and thus lacks only a small area of presumed calcification in the nasal region; posteriorly much of the endolymphatic slit is present, and hence there has been lost only the short occipital region and the posterior end of the otic region (with the otic processes). The specimen is somewhat larger than *Tamiobatis*, but resembles that type closely in general proportions in both dorsal and ventral views, and has the great advantage of being uncrushed. Whereas, for example, this *Cladodus* specimen is but 20 per cent or so larger than *Tamiobatis* in dimensions measured on both upper and lower surfaces, its height at (for example) the level of the postorbital processes is approximately double that of the *Tamiobatis* type.

As may be seen by comparing Gross' figure 1 with Figure 1 of this paper, his braincase is in dorsal view very similar to that of *Tamiobatis*. Both show the notch for an anterior fontanelle, a broad interorbital region forming laterally a roof for the large orbit, and a row of nerve foramina for the supraorbital lateral line canal. In both there is a prominent postorbital process (somewhat imperfect dorsodistally in the Gross specimen). In this specimen we find definite proof that — in contrast to Stensiö's assumption — there was a greatly elongated otic region. As in *Tamiobatis*, there is a well-marked area of the dorsal ridges such as I believe were apposed to the palatoquadrates. Centrally and posteriorly there is an elongate endolymphatic opening like that of *Tamiobatis*. As in that form, a swelling (*hB*) posterolateral to that opening is obviously related to the posterior vertical canal, thus showing that in "*Cladodus*," contrary to Stensiö's interpretation of a much poorer specimen, the canal region was greatly elongate. Dorsally, Gross' specimen becomes imperfect posteriorly before the end of the endolymphatic slit is reached. He tends to assume (presumably influenced by a comparison with modern sharks) that the terminus of the roof of the braincase had been nearly attained at this point. But comparison with *Tamiobatis* strongly suggests that a considerable area is absent here, including projecting otic processes. It is unfortunate that it cannot be said whether the dorsal ridges terminated in the prominent posteriorly-projecting processes seen in *Tamiobatis* and pleuracanths.

Ventrally, Gross' specimen again compares closely with *Tamiobatis;* his figure 5 (except for the absent otic processes) compares closely with my Figure 4.

The structure of the orbital region, seen in Gross' figures 3A and 3B, is comparable in most respects to Stensiö's findings and those seen in *Tamiobatis* (Fig. 2). In all three there is a prominent oval for an eye stalk, an optic nerve foramen anterior to it, and more dorsally, foramina for nerves III and IV. As in the case of Stensiö's specimen, Gross was able to make out ventral foramina for an ophthalmic artery and pituitary vein — structures which crushing appears to have obliterated in *Tamiobatis*. In *Tamiobatis* there appears to be a single opening in the posterodorsal corner of the orbit for ophthalmic rami; in *C. wildungensis* there are two distinct openings here (*O Sup*, *O Sup?*). I am unable to completely reconcile the foramina for various elements of V and VII as determined by Gross with those which I appear to find in *Tamiobatis* or those identified by Stensiö. As in *Tamiobatis*, but in disagreement with Stensiö's description of his specimen, there is but a single anteroposterior canal traversing the base of the postorbital process. As noted above, the postorbital process was incompletely preserved in *C. hassiacus;* that in *C. wildungensis* agrees well with that of *Tamiobatis* in the presence of a canal for the pretrematic ramus of the facialis and a distinct articular area for the palatoquadrate.

In sum, apart from a few differences regarding nerve foramina, possibly due to imperfections in the materials, the braincase described by Gross agrees in almost every preserved feature with *Tamiobatis*. It is obvious, assuming that *Cladodus wildungensis* and *Cladodus hassiacus* are really related, that the proportions attributed by Stensiö to the braincase in his specimen are (literally) far short of the truth as regards its length.

As noted earlier, I have long had in my possession considerable materials of "*Pleuracanthus*" from the Lower Permian of Texas, and had, a number of years ago, begun a study of the braincase, including the serial sectioning of a number of specimens. I hope to complete this study in the not distant future, and will postpone any detailed comparison of this material with *Tamiobatis* and "*Cladodus*" until this has been done. It may be said in the meantime, however, that as far as can be seen at present, agreement is very close. If such a figure as that of the dorsal surface of the pleuracanth skull published by me in 1933 (fig. 26; 1945, fig. 55)[1] be compared with that of *Tamiobatis*, it will be seen that the two are similar in all general regards (except for a somewhat greater lateral projection of the otic processes in *Tamiobatis*), and the same holds true for many other features of the anatomy.

## CONCLUSION

I had at one time thought that, due to the great similarity between the pleuracanths and *Tamiobatis*, the latter might be an early representative of the pleuracanth group. Against this is the fact that pleuracanths are mainly freshwater forms,

[1] Hussakof's figures of this skull type (1911, pl. 29) are grossly inaccurate, in a fashion similar to Eastman's misinterpretation of *Tamiobatis*, with dorsal and ventral surfaces reversed, the postorbital process identified as nasal capsule, etc.

whereas *Tamiobatis* is from a marine limestone. This is not a crucial argument, for the later pleuracanths may well have migrated from salt water to fresh, and *Tamiobatis* might have been an ancestral marine form. But since the "*Cladodus*" specimens are, as far as known, in essential agreement with *Tamiobatis* and the pleuracanths, it is more reasonable to believe that we are here dealing with a truly primitive elasmobranch type of braincase, characteristic of ancestral shark types in the Devonian, not improbably retained in more generalized Carboniferous forms, and persistently retained by the pleuracanth side-branch of the shark group.

The most conspicuous difference between this type of primitive shark braincase and that of modern genera is, of course, the very long otic and occipital segments of the primitive braincase, with the more "expansive" development of the braincase cartilages to include the anterior part of the dorsal aorta within its substance. So radical are the differences in proportion here that it was not surprising that, in default of more complete material, Stensiö restored his *Cladodus* specimen in abbreviate modern fashion. I regard it as highly probable that all later elasmobranchs are descended from Triassic hybodonts; in these forms shortening of the otic region had already occurred (cf. *Hybodus*, as figured by Smith Woodward, 1916, fig. 3). It is to be hoped that further discoveries of Paleozoic sharks may at some future time give us knowledge of the phylogenetic point at which this shortening occurred, and of the associated functional "reasons" (no doubt complex). It is of interest, in view of the belief of many that the elasmobranchs are allied to the placoderms, that in many members of that important Devonian group the "facial" region was, as in the older sharks, relatively short, and the otic plus occipital regions often greatly elongated. The change in proportions seen in the evolutionary history of the elasmobranch "skull" may well be merely one of a number of parallel developments in this regard in higher fishes and lower tetrapods. For example, the long-standing confusion as to the nomenclature of the dermal roofing elements of the frontal-parietal regions in rhipidistians was due to the fact that in the evolutionary series rhipidistians – amphibians – reptiles there was a long-continued trend toward relative reduction of the otico-occipital region, with a concomitant rearrangement of the overlying dermal elements (Westoll, 1938; see Romer, 1941, fig. 4).

One thus gains the impression that there has been, in the history of the gnathostome fishes, a strong trend toward relative reduction of the posterior portion of the cranial structures and, very probably, a concomitant elaboration of the "facial" region. Study of the functional changes which underlie this trend may be worthy of pursuit.

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(Received August 26, 1963)